ON THE EMBRYONIC DEVELOPMENT OF THE SEA URCHIN ALLOCENTROTUS FRAGILIS[1]

A. R. MOORE

Hopkins Marine Station of Stanford University, Pacific Grove, California

Allocentrotus fragilis, thanks to its brightly colored test and whitish short spines, has been termed the most beautiful of the sea urchins. Perhaps because of the fragility of the almost paper-thin test and the depths at which this sea urchin lives there was no study of the species before that of Jackson in 1912. He gave it the name *Strongylocentrotus fragilis.* In 1943 Mortensen, in his revision, assigned to the species a new generic title, *Allocentrotus* (Boolootian *et al.*, 1959).

The first specimens taken in any quantity at the Pacific Grove station were dredged from depths of 80 to 100 fathoms, temperature approximately 8° C. Although samples were taken throughout the year, I have found ripe eggs only in February and March. Animals dredged in mid-April showed that complete spawning had taken place, with the exception of one male which yielded a little active sperm. The animals lived very well for at least two weeks in aquaria of the laboratory in which the temperature of the running sea water was approximately 14° C. Eggs and sperm were taken from these animals from time to time. The specimens used were from 50 to 80 mm. in diameter. Only one of those taken during the three seasons equaled in diameter the largest recorded by Clark (1948), namely a little over 100 mm. The test of this specimen is in the collection of Dr. J. Wyatt Durham of the Department of Paleontology, University of California, Berkeley.

Eggs and sperm were first obtained by opening the animals and putting the gonads into dishes of sea water into which the sex products quickly escaped. Later, in order to avoid waste, the electrical method (Harvey, 1953) was used and found to be very satisfactory. The eggs are very light in color, so that, as they stream out of the ovary they may at first be mistaken for sperm. The diameter of the egg is approximately 110 μ which is midway between the dimensions of the eggs of the two shore forms, *Strongylocentrotus purpuratus* (78 μ) and *Strongylocentrotus franciscanus* (140 μ). The fertilization membrane closely invests the egg, being in distance from the egg's surface $\frac{1}{16}$ the diameter of the egg (Fig. 1). In contrast the fertilization membrane of *S. purpuratus* is removed from the surface of the egg $\frac{1}{6}$ the diameter of the egg.

At a given temperature, the eggs of *Allocentrotus fragilis* divide at exactly the same rate as those of the two shore forms *Strongylocentrotus purpuratus* and *S. franciscanus.* The temperature for successful development of *Allocentrotus fragilis* must be kept at 15° C. or lower (Moore, 1959) (Figs. 1–4). There is, however, some variation, the eggs of an occasional individual segmenting normally at 16°

[1] Identified for me by Dr. J. Wyatt Durham.

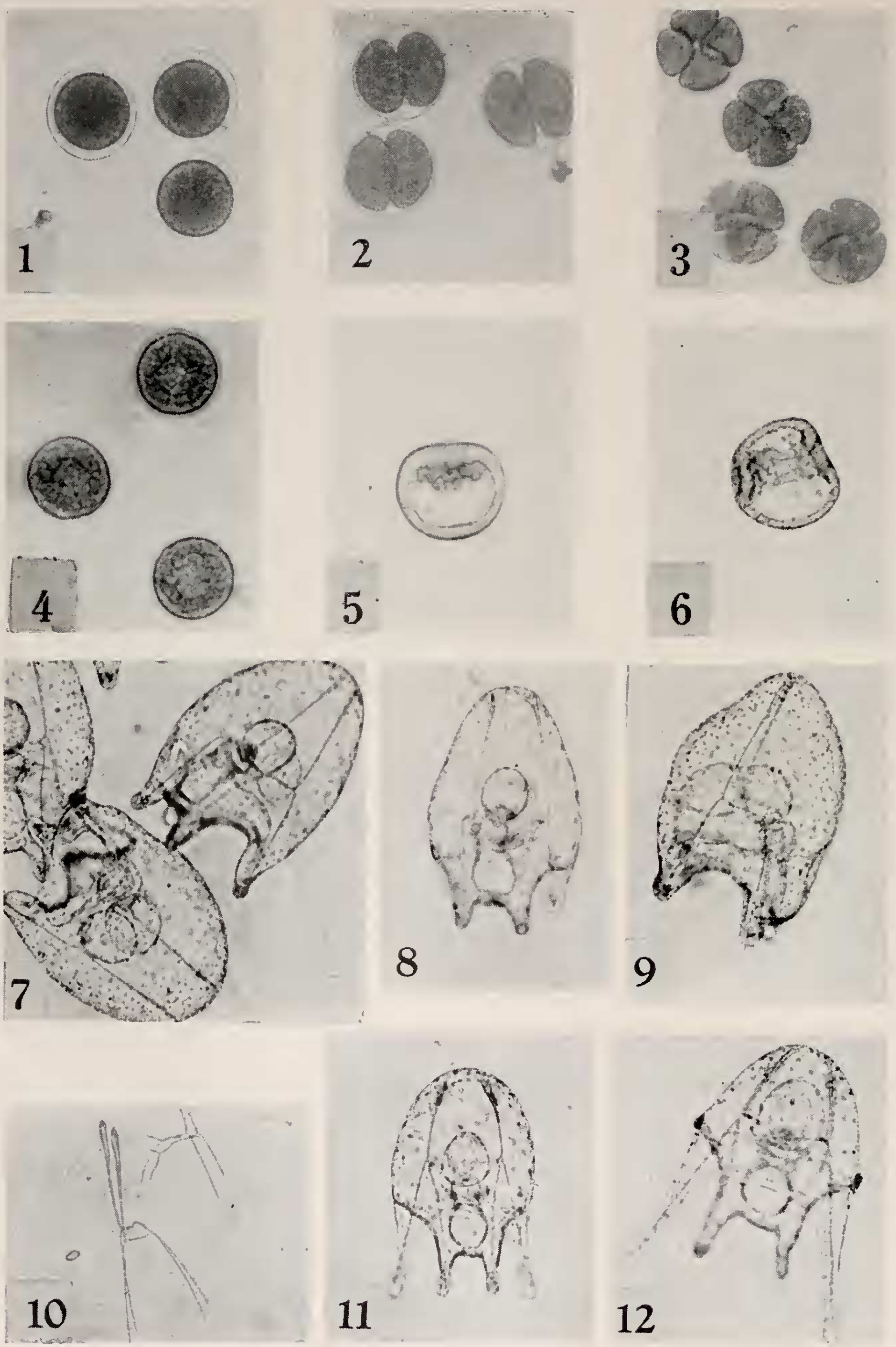
or even 17° C. while others require 14° C. or lower for successful development.

The blastulae (Fig. 5) early show flattening at the poles, in that way differing from the oval form of the same stage in *S. purpuratus*. The pluteus, which is formed three days after fertilization, resembles that of *S. purpuratus* in having short arms, but the shape of the body is somewhat cylindrical and thus differs from that of *S. purpuratus* which is conical or pyramidal in shape (Figs. 7, 8, 9). The skeleton (Fig. 10) resembles that of *S. purpuratus* in the club-shape of the body-rods, in its smoothness and in the short post-oral rods; the cross-bars are absent. In general the skeleton is thinner than that of *S. purpuratus*. An accessory post-oral rod is frequently present. In contrast to the comparatively simple structures of these two forms, the pluteus of *S. franciscanus* is more elaborate in that it is characterized by long arms, the presence of cross-bars and thorniness of the body-rods at the apex (Fig. 12).

Cross-fertilization with the two shore forms succeeded especially well in February. The eggs of *S. purpuratus* fertilized with the sperm of *A. fragilis* gave more than 50 per cent fertilization as did the reciprocal cross. The differences between the two forms in the characters of the pluteus are so slight that no study of these hybrids was made at this time. The case is different in the cross *A. fragilis* ♀ × *S. franciscanus* ♂. Here the percentage of the eggs fertilized varied between 20 and 50 per cent. Figure 11 illustrates a pluteus of this hybrid. The lengthening of the arms, the presence of cross-bars and thickening of the apical skeleton are the chief features derived from the male parent (Fig. 12). The hybrid therefore has longer arms and more complex skeleton than the maternal species by virtue of characters inherited from the male parent, and therefore follows the pattern of the cross *S. purpuratus* ♀ × *S. franciscanus* ♂ (Moore, 1943).

Discussion

The deep water sea urchin, *Allocentrotus fragilis* has been taken at depths of 40 to 417 fathoms from Vancouver Island to Pt. Santa Eugina in Lower California (Clark, 1948). The species thus can thrive at a very low temperature and in the absence of light. The short breeding season, February and March, raises the question of the triggering of spawning, which takes place promptly at the end of March or beginning of April. This is the record of three successive seasons at the Pacific Grove station, and leads one to believe that spawning is, for some reason, associated with the onset of spring. Increase of light or temperature as causative factors would seem to be excluded because of the conditions at the great depths at which this species flourishes. Pertinent to the question of the triggering of spawning is the fact that ripe individuals have been kept in laboratory aquaria at a temperature of approximately 14° C. for two weeks or longer without their showing any evidence of spawning. During the time the animals retained their spines, they yielded eggs and sperm. Thus, a sudden increase in temperature and abundant light did not show any effect of triggering the spawning of ripe individuals. As to the cause of spawning in the natural habitat, there is the possibility in the spring flowering of the plankton algae. Thorson (1946) has suggested that these algae may, by their fall to the bottom, yield algal extracts which furnish the chemical trigger for spawning. There remains the possibility



Figures 1–12.

that this animal, as a character of its being, has an annual periodicity which is independent of environmental factors.

The close relationship of *Allocentrotus fragilis* to the two shore forms of *Strongylocentrotus* is indicated, first, by the exact time relations of development, which are precisely the same in the three species, and by the fact that crosses can easily be made between *Allocentrotus fragilis* and the two species of *Strongylocentrotus*. The inheritance of paternal characters in the cross *Allocentrotus fragilis* ♀ × *S. franciscanus* ♂ proves that we have here true fertilization and not parthenogenesis.

It gives me pleasure to record my cordial thanks to Mr. Tom Fast who made the initial discovery of the bed of *Allocentrotus fragilis* at Pacific Grove in February, 1957, and who gave me the entire number taken at that time. Subsequent hauls were made by junior members of the Station staff who very graciously furnished me with specimens needed for my work.

Summary

1. Ripe eggs and sperm of *Allocentrotus fragilis* were obtained during February and March, from animals taken at depths of 80 to 100 fathoms.

2. Fertilization was approximately 100 per cent, and development was normal at a temperature of 15° C. or lower.

3. The rate of development in *Allocentrotus fragilis* is identical to that of the two species of *Strongylocentrotus* at this locality.

4. The pluteus has a characteristic form which distinguishes it from those of *S. purpuratus* and *S. franciscanus*.

5. Cross-fertilization between *Allocentrotus fragilis* and the two forms of *Strongylocentrotus* was accomplished, and in the progeny of *A. fragilis* ♀ × *S. franciscanus* ♂ the development of paternal characters was clearly shown.

6. As to the cause of spring spawning, increase in light and possible increase in temperature are not factors, but Thorson's idea of the occurrence of algal extracts of the plankton in early spring is suggested as a possible factor. There is also the possibility of an innate periodicity characteristic of the species.

LITERATURE CITED

Boolootian, R. A., A. C. Giese, J. S. Tucker and A. Farmanfarmaian, 1959. A contribution to the biology of a deep sea echinoid, *Allocentrotus fragilis* (Jackson). *Biol. Bull.*, **116**: 362–372.

Figures 1 to 10 inclusive refer to *Allocentrotus fragilis*. Magnification 100 ×.

Figure 1. Fertilized egg.
Figures 2, 3. Segmentation stages, 2-cell and 4-cell.
Figure 4. Blastula before hatching.
Figure 5. Swimming blastula, 24 hours.
Figure 6. Gastrula, 48 hours.
Figures 7, 8, 9. Plutei, 5 days.
Figure 10. Skeleton of pluteus of *Allocentrotus fragilis*.
Figure 11. Pluteus of hybrid *Allocentrotus fragilis* ♀ × *Strongylocentrotus franciscanus* ♂, 5 days.
Figure 12. Pluteus of *Strongylocentrotus franciscanus*, 5 days.

CLARK, H. L., 1948. A report on the echini of the eastern Pacific, based on the collections of Valero III. Univ. of Southern California press, pp. 276–277.

HARVEY, E. B., 1953. A simplified electrical method of determining the sex of sea urchins and other marine animals. *Biol. Bull.*, **105**: 365.

JACKSON, M. T., 1912. Phylogeny of the Echini. *Mem. Boston Soc. Nat. Hist.*, **7**: 128.

MOORE, A. R., 1959. Some effects of temperature on embryonic development in the sea urchin *Allocentrotus fragilis*. *Biol. Bull.*, **117**: 150–153.

MOORE, A. R., 1943. Maternal and paternal inheritance in the plutei of the sea urchins *Strongylocentrotus purpuratus* and *S. franciscanus*. *J. Exp. Zool.*, **94**: 211–228.

MORTENSEN, TH., 1943. A monograph of Echinoidea III, Camerodonta II. Copenhagen, C. A. Reitzel Publ. pp. 446. Ref. 255–258.

THORSON, GUNNAR, 1946. Reproduction and larval development of Danish marine bottom invertebrates. *Medd. Komm. Dann. Fiskerei og Havunders, ser. Plankton*, **4**: 1–523. Ref. pp. 423–425.